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Research Article

Soil Zinc Availability Alters the Contribution of Pre-Anthesis and Post-Anthesis Uptake in Rice Grain Zinc Loading

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ABSTRACT

Rice (*Oryza sativa* L.) is the most crucial cereal globally and serves as a vital source of zinc (Zn) for individuals whose diets are primarily rice-based. To improve the Zn content in rice, it is essential to gain a deeper understanding of how plants absorb and distribute zinc internally. This research investigated how different rates of soil Zn fertilization (0, 3, 6, 9, 12, and 15 kg Zn ha⁻¹) impacted the growth, yield, zinc uptake, and remobilization in the non-aromatic rice genotype '10/B-2-1', cultivated in Zn-deficient soil. The findings indicated that zinc application had a notable influence on rice yield and related parameters, except for the tiller count per plant and panicle length. The concentration and accumulation of zinc at both anthesis and maturity showed significant increases, particularly at higher zinc rates (9, 12, and 15 kg Zn ha⁻¹) compared to the control. Over 85% of the zinc accumulated at maturity came from uptake prior to anthesis. Additionally, the efficiency of zinc remobilization dropped from 22.28% in the control to 10.88% at the highest zinc application of 15 kg Zn ha⁻¹. The proportion of grain zinc derived from remobilization significantly decreased from 65.66% to 40.29% as zinc levels rose from 0 to 15 kg Zn ha⁻¹, highlighting the critical role of post-anthesis uptake in grain Zn loading when zinc availability is higher. Moreover, it was evident that post-anthesis uptake was the principal source of grain Zn when AB-DTPA extractable zinc concentrations exceeded 1.0 mg kg⁻¹, while pre-anthesis remobilization prevailed at lower soil zinc concentrations. The results of study warrant further investigations involving larger number of genotypes on diverse soil types.

Keywords: Soil critical Zn level, Zn accumulation, Zn fertilization, Zn remobilization.



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INTRODUCTION

Zinc (Zn) deficiency is an important micronutrient concern in cereal crops, leading to reduced yields and nutritional quality (Rehman et al., 2018). Around 50% of cereal crops globally are grown in Zn-deficient soils (Cakmak and Kutman, 2018), impacting human health, particularly in developing nations where cereals are dietary staples (Gupta et al., 2020). Biofortification of staple foods, especially through Zn fertilization, offers a short-term solution to improve Zn content (Praharaj et al., 2021). While new crop varieties with enhanced Zn absorption are being developed, soil Zn availability remains crucial (Liu et al., 2019), often supplemented by zinc sulfate application (Cakmak, 2008).

Rice (*Oryza sativa* L.), a primary food source for over half the global population, is low in essential micronutrients like Zn due to limited soil Zn bioavailability (Phuphong et al., 2020). Zinc deficiency occurs due to precipitation or adsorption with soil components, which varies with soil pH and redox potential (Johnson-Beebout et al., 2016). In rice, Zn deficiency causes chlorosis in leaves, leaf size

reduction, short internodes, and root necrosis, leading to stunted growth and yield loss. The Zn content in all portions of the rice plant including kernel and straw is appreciably increased through the application of Zn fertilizers in the soil (Verma et al., 2022).

Increasing Zn contents in rice involves various physiological steps like root absorption, translocation to shoots, and remobilization (Gupta et al., 2016). Understanding these stages can improve our strategies for enhancing grain Zn content through genetic and agronomic methods. Zn remobilization from shoots or roots and continuous root uptake during grain filling are the two primary kinds of zinc accumulation mechanisms in rice (Yin et al., 2016). It is unclear what factors influence these mechanisms and how they differ among rice genotypes chosen for high Zn contents. There are differing opinions about the sources of grain Zn loading; some studies highlight remobilization from source tissues (Wu et al., 2010), while others highlight ongoing root uptake as the primary source (Jiang et al., 2007). Additionally, the main Zn loading source is influenced by Zn availability and genetic differences among rice varieties (Impa et al., 2013a). Certain Zn-efficient genotypes are better at remobilizing Zn from older to new tissues than those susceptible to deficiency (Impa et al., 2013b; Kaur et al., 2021). When zinc uptake continues after blooming, both pre- and post-flowering zinc uptake have a considerable role in grain zinc loading (Stomph et al., 2014). Furthermore, rice genotypes' zinc absorption behavior has a major impact on the movement of zinc from soil to grain, which is crucial for overcoming biofortification obstacles (Johnson-Beebout et al., 2016). It is essential to note that all of the aforementioned studies involved pot or hydroponic experiments, necessitating further evaluation in field conditions. Additionally, the threshold of soil Zn availability that influences predominance of Zn remobilization or uptake in rice crop has yet to be established for different soil types under field environments.

The present field experimentation examined the effects of soil zinc fertilization on Zn uptake at pre- and post-anthesis stages, and remobilization by the lowland rice. The specific goals were to ascertain how soil zinc application affected (1) zinc uptake by aboveground plant parts and (2) the degree to which pre-anthesis Zn remobilization and post-anthesis Zn uptake contributed to grain zinc as influenced by zinc fertilization rates.

MATERIALS AND METHODS

Experimental location, design and treatments

This study was conducted in the kharif season of 2022 using a randomized complete block design with five levels of zinc (0, 3, 6, 9, 12, and 15 kg ha⁻¹) and three replications. The experimental soil was characterized as non-saline (EC_{1:2.5} = 1.05 dS m⁻¹), alkaline (pH = 7.8), and clayey in texture (sand 27.23%, silt 25.55%, and clay 47.22%) according to the USDA soil classification system. It was short in organic matter (0.69%), total nitrogen (0.033%), AB-DTPA-extractable phosphorus (6.1 mg kg⁻¹), and zinc (0.43 mg kg⁻¹), while the AB-DTPA-extractable potassium (165 mg kg⁻¹) was within the adequate range. The size of each experimental unit was 4 m × 4 m (16 m²). Zinc was applied in the form of zinc sulfate monohydrate (ZnSO₄ · H₂O, 35%). All of the phosphorus (60 kg P₂O₅ ha⁻¹ in the form of triple super phosphate) and potassium (25 kg K₂O ha⁻¹ in the form of sulfate of potash) were used at the time of transplanting while Zn was applied after 20 days of transplanting in order to minimize the interaction between applied phosphorus and zinc. Nitrogen in the form of urea were used in three equal splits viz., at transplanting, at 50% tillering and at panicle initiation stage. The study utilized a promising high yielding rice genotype '10/B-2-1' as a test crop.

Crop husbandry

On July 5, 2022, twenty-five-day-old seedlings were transplanted into the field. The transplanting was done with two seedlings per hill, maintaining a row to row and plant to plant spacing of 20 cm. Prior to transplanting, the nursery bed was thoroughly irrigated to facilitate easier uprooting of the seedlings, which were then carefully washed before being transplanted. After transplanting, various crop husbandry management practices viz., water management, pest control, and weed management, were implemented as required to ensure optimal growth conditions. The crop rice was harvested once the ears had nearly ripened, indicated by the straw turning a golden yellow color, signaling the crop's readiness for harvest.

Sampling and measurements

To determine Zn remobilization, one entire row from the center of the each plot was harvested at the anthesis stage. Five plants were randomly chosen from each experimental unit at crop maturity, and their heights were measured using a meter rod from the base of the stem to the top of the panicle of the tallest culm, then averaged. The panicles from the primary tillers were cut using scissors to measure their lengths from the panicle neck to the tip of the uppermost branch, and the number of tillers on the chosen plants was tallied. To determine how many grains each

panicle contained, each panicle was manually threshed. To determine the grain yield, the grains from these panicles were combined with the remaining output from the corresponding experimental unit. Plant material from each experimental unit was harvested, and manually threshed to separate the grains from the straw. A top-loading digital balance was used to record the grain weight of one hundred randomly selected kernels. The dry matter basis (weighed after 48 hours of drying at 70 °C) was used in this study to express the yields of shoots, grain, and straw. A stainless steel grinder was then used to grind the plant material (straw, grain, and shoot) that had been oven-dried. Following digestion with perchloric acid-nitric acid, the Zn content of the finely ground plant samples was determined using an atomic absorption spectrophotometer (Jones and Case, 1990). After crop harvest, composite soil samples from the 0–20 cm surface layer were taken from each experimental unit with a stainless steel auger. The air-dried soil samples were crushed using a wooden pestle and mortar and sieved through a 2-mm screen. Ammonium bicarbonate-diethylenetriamine pentaacetic acid (AB-DTPA) was used to extract the soil samples (Soltanpour and Workman, 1979) and an atomic absorption spectrophotometer was used to determine the extracts' zinc concentration.

Calculations and statistics

The following parameters related to Zn accumulation and remobilization were calculated by following the formulas of Liu et al. (2019):

Zn accumulation (shoot / grain / straw) (g ha^{-1}) =

$$\text{Zn concentration (shoot / grain / straw) (mg/kg)} \times \text{Biomass (shoot / grain / straw) (t/ha)}$$

Total Zn accumulation at maturity (g ha^{-1}) =

$$\text{Grain Zn accumulation (g/ha)} + \text{Straw Zn accumulation (g/ha)}$$

Post-anthesis Zn accumulation (g ha^{-1}) =

$$\text{Total Zn accumulation at maturity (g/ha)} - \text{shoot Zn accumulation at anthesis (g/ha)}$$

Pre-anthesis or post-anthesis Zn accumulation (%) =

$$\frac{\text{Zn accumulation at anthesis or post - anthesis (g/ha)}}{\text{Total Zn accumulation at maturity (g/ha)}} \times 100$$

Zn remobilization to grain (g ha^{-1}) =

$$\text{Shoot Zn accumulation at anthesis (g/ha)} - \text{Straw Zn accumulation (g/ha)}$$

Zinc remobilization efficiency (%) =

$$\frac{\text{Zn remobilization to grain (g/ha)}}{\text{Shoot Zn accumulation at anthesis (g/ha)}} \times 100$$

Grain zinc contribution from remobilization (%) =

$$\frac{\text{Zn remobilization to the grain (g/ha)}}{\text{Grain Zn accumulation (g/ha)}} \times 100$$

Grain zinc contribution from post-anthesis Zn accumulation (%) =

$$\frac{\text{Grain Zn accumulation (g/ha)} - \text{Zn remobilization to grain (g/ha)}}{\text{Grain Zn accumulation (g/ha)}} \times 100$$

Analysis of variance was used to examine the data on different growth, yield, and zinc-related attributes within the context of randomized complete block design. As per Gomez and Gomez (1984), Tukey's Honestly Significant Difference (HSD) test was used at significance level of 5% to distinguish between the treatment means.

RESULTS

Yield and yield contributing attributes of rice genotype

Plant height increased significantly when Zn was applied to the soil at rates of 3, 6, 9, 12, and 15 kg ha^{-1} compared to the control (no Zn application) (Table 1). The highest plant height (130.7 cm) was achieved by a treatment of 12 kg Zn ha^{-1} , however this treatment was statistically comparable to all other Zn application levels (3, 6, 9, and 15 kg ha^{-1}). The length of the panicle and the tiller count per plant were not significantly affected by zinc application. When zinc was applied at higher rates, the grains number per panicle and 100- weight of grain improved significantly as well. By the application of 15 kg Zn ha^{-1} , the greater grains number per panicle (212.3) and 100-grain weight (2.89 g) were achieved, but the statistical similarity of this treatment with all other treatments except control was noted (Table 1).

Table 1. Yield contributing parameters of rice genotype as affected by Zn application rates.

Treatments	Plant height (cm)	No. of tillers per plant (No.)	Panicle length (cm)	No. of grains per panicle (No.)	Hundred grain weight (g)
Control	120.6 b	7.8 ns	28.6 ns	177.3 b	2.51 b
3 kg Zn ha ⁻¹	124.9 ab	7.9	29.4	187.3 ab	2.75 ab
6 kg Zn ha ⁻¹	127.7 ab	8.4	30.7	195.3 ab	2.80 a
9 kg Zn ha ⁻¹	127.6 ab	8.7	30.6	195.0 ab	2.87 a
12 kg Zn ha ⁻¹	130.7 a	9.0	31.0	210.3 ab	2.87 a
15 kg Zn ha ⁻¹	129.9 a	9.2	31.2	212.3 a	2.89 a
HSD_{0.05}	8.86	1.58	3.32	34.46	0.27

HSD_{0.05} = Honestly Significant Difference at 5% probability level

At the anthesis stage, the shoot biomass of the rice genotype ranged from 13.49 to 15.43 t ha⁻¹. The 15 kg Zn ha⁻¹ applied in the soil resulted in the highest shoot biomass production, achieving a notable increase of 14.36% compared to the control, which did not receive any zinc treatment. Interestingly, this increase in biomass with 15 kg Zn ha⁻¹ was statistically comparable to the biomass observed with lower zinc application rates of 3, 6, 9, and 12 kg Zn ha⁻¹, suggesting that even lower zinc dosages were successful in increasing shoot biomass to a comparable degree (Table 2).

Table 2. Shoot, grain and straw yield of rice genotype as affected by Zn application rates.

Treatments	At anthesis	At maturity	
	Shoot (t ha ⁻¹)	Grain (t ha ⁻¹)	Straw (t ha ⁻¹)
Control	13.49 b	6.60 b	12.80 b
3 kg Zn ha ⁻¹	14.22 ab	7.10 a	13.81 ab
6 kg Zn ha ⁻¹	14.79 ab	7.16 a	13.97 ab
9 kg Zn ha ⁻¹	15.20 a	7.20 a	13.94 ab
12 kg Zn ha ⁻¹	15.26 a	7.18 a	15.10 ab
15 kg Zn ha ⁻¹	15.43 a	7.30 a	15.54 a
HSD_{0.05}	1.32	0.41	2.55

HSD_{0.05} = Honestly Significant Difference at 5% probability level

The 15 kg Zn ha⁻¹ applied to the soil enhanced the grain yield of rice genotype from 6.60 to 7.30 t ha⁻¹; this treatment was statistically equal to treatments with 3, 6, 9 and 12 kg Zn ha⁻¹. Table 2 shows that the percentage improvements in yield over the control treatment were 7.58, 8.60, 9.12, 8.88, and 10.66% with the application of 3, 6, 9, 12, and 15 kg Zn ha⁻¹. The rice genotype's straw yield varied from 12.50 to 15.54 t ha⁻¹, with the largest yield recorded and a 21.36% increase over the control when 15 kg Zn ha⁻¹ was applied to the soil. The effect of this treatment was statistically comparable to that of 3, 6, 9, and 12 kg Zn ha⁻¹.

Zn concentration at anthesis and maturity stage

The zinc concentration in shoot at anthesis showed a significant increase when zinc was applied to the soil, compared to the control treatment where no zinc was added (Table 3). Across the different levels of zinc application, the shoot zinc concentration ranged from 37.77 to 59.69 mg kg⁻¹, the highest zinc concentration being observed at 15 kg Zn ha⁻¹. However, this maximum zinc concentration was statistically similar to the zinc content recorded at lower rates of 9 and 12 kg Zn ha⁻¹, indicating that these lower application rates were nearly as effective in enhancing shoot zinc content as the highest application rate.

After applying zinc to the soil, there were a notable rise in the concentration of Zn in grains and straw when compared to the control. Grain zinc concentration ranged from 26.42 to 38.73 mg kg⁻¹, with the maximum content at a rate of 15 kg ha⁻¹, that were statistically comparable to treatments applying 9 and 12 kg ha⁻¹ of zinc (Table 3). In straw, the concentration of zinc extended from 30.93 to 51.90 mg kg⁻¹. The highest concentration of zinc was achieved with a 15 kg ha⁻¹ application, which did not significantly differ from the treatment that received 9 and 12 kg ha⁻¹ (Table 3).

Table 3. Zn concentration and accumulation at anthesis and maturity as affected by Zn application rates.

Treatments	Zn concentration (mg kg ⁻¹)			Zn accumulation (g ha ⁻¹)		
	At anthesis	At maturity		At anthesis	At maturity	
	Shoot	Grain	Straw	Shoot	Grain	Straw
Control	37.77 d	26.42 d	30.93 d	509.6 d	174.3 c	396.1 e
3 kg Zn ha ⁻¹	44.22 cd	30.24 cd	36.11 cd	628.7 cd	214.7 bc	499.5 de
6 kg Zn ha ⁻¹	47.41 bcd	32.63 bc	42.24 bc	702.4 bc	234.4 ab	587.4 cd
9 kg Zn ha ⁻¹	50.86 abc	33.87 abc	47.52 ab	777.2 abc	243.0 ab	662.6 bc
12 kg Zn ha ⁻¹	55.75 ab	37.45 ab	48.01 ab	850.5 ab	268.5 ab	726.4 ab
15 kg Zn ha ⁻¹	59.69 a	38.73 a	51.90 a	918.5 a	282.9 a	808.1 a
HSD_{0.05}	10.34	5.90	8.41	176.4	57.0	138.4

HSD_{0.05} = Honestly Significant Difference at 5% probability level

Zn accumulation at anthesis and maturity stage

The amount of zinc accumulated in the shoot increased significantly with each increment in zinc application rate (Table 3). With Zn application @ 15 kg ha⁻¹, the Zn accumulation in shoot reached its highest (918.5 g ha⁻¹), although it was statistically similar to the treatments with 9 and 12 kg Zn ha⁻¹. This suggests that while significant zinc accumulation was also facilitated by lower application rates, the largest accumulation was attained with the highest zinc application.

With the exception of 3 kg Zn ha⁻¹, Zn application in soil greatly enhanced the Zn accumulation in rice grain and straw compared to the control. The amount of zinc accumulated in grain ranged from 174.3 to 282.9 g ha⁻¹, with the maximum amount occurring at a rate of 15 kg ha⁻¹. Nevertheless, it was statistically comparable to treatments with 6, 9, and 12 kg Zn ha⁻¹ (Table 2). With every increase in Zn application, there was a significant ($P < 0.05$) rise in the Zn accumulation in straw. While it was statistically comparable to treatment with 12 kg Zn ha⁻¹, accumulation in straw reached its highest (808.1 g ha⁻¹) with Zn application @ 15 kg ha⁻¹ (Table 3).

Grain Zn accumulation via pre-anthesis remobilization vs. post-anthesis uptake

A review of the data revealed that more than 85% of the total Zn accumulation at maturity occurred before the pre-anthesis stage at all Zn application rates (Table 4). When Zn rate was increased from 0 to 15 kg ha⁻¹, the contribution of pre-anthesis Zn accumulation to the total Zn accumulation (grain + straw) at maturity dropped from 89.48 to 85.15%, however the decline was not statistically significant. On the other hand, the contribution of post-anthesis Zn accumulation significantly increased from 10.52 to 14.85 % with the application 15 kg Zn ha⁻¹. Zinc remobilization to the grain was also greatly impacted by Zn application rates, with the highest (129.2 g ha⁻¹) and lowest (110.4 g ha⁻¹) values noted at 3 and 15 kg Zn ha⁻¹, respectively. In a similar way, Zn application rate led to a decrease in Zn remobilization efficiency (Table 4). When the Zn application rate was raised from 0 to 15 kg ha⁻¹, the share of post-anthesis Zn uptake increased from 34.34 to 59.71%, while the share of grain Zn supplied via remobilization reduced from 65.66 to 40.29%.

Table 4. Zinc remobilization related parameters of rice genotype as affected by Zn application rates.

Treatments	Zn accumulation ratio (%)		Zn remobilization to grain (g ha ⁻¹)	Zn remobilization efficiency (%)	Share of grain Zn provided by remobilization (%)	Share of post-anthesis shoot Zn uptake to grain Zn (%)
	Pre-anthesis	Post-anthesis				
Control	89.48 ns	10.52 b	113.5 ab	22.28 a	65.66 a	34.34 b
3 kg Zn ha ⁻¹	88.37	11.63 ab	129.2 a	20.57 ab	61.69 ab	38.31 ab
6 kg Zn ha ⁻¹	85.59	14.41 ab	115.0 ab	15.57 abc	47.41 ab	52.59 ab
9 kg Zn ha ⁻¹	85.50	14.50 a	114.6 ab	12.87 bc	47.73 ab	52.27 ab
12 kg Zn ha ⁻¹	86.20	13.80 ab	124.1 ab	14.54 abc	48.30 ab	51.70 ab
15 kg Zn ha ⁻¹	85.15	14.85 a	110.4 b	10.88 c	40.29 b	59.71 a
HSD_{0.05}	12.85	3.96	17.77	8.24	21.86	22.31

HSD_{0.05} = Honestly Significant Difference at 5% probability level

The percentage of rice grain zinc originating from pre-anthesis remobilization and post-anthesis Zn uptake was correlated with soil AB-DTPA extractable zinc at maturity. This suggested that when AB-DTPA Zn levels were higher than 1.0 mg kg^{-1} , Zn absorption/uptake was significant than remobilization. On the other hand, when AB-DTPA Zn levels were less than 1.0 mg kg^{-1} , remobilization significantly outweighed absorption (Figure 1).

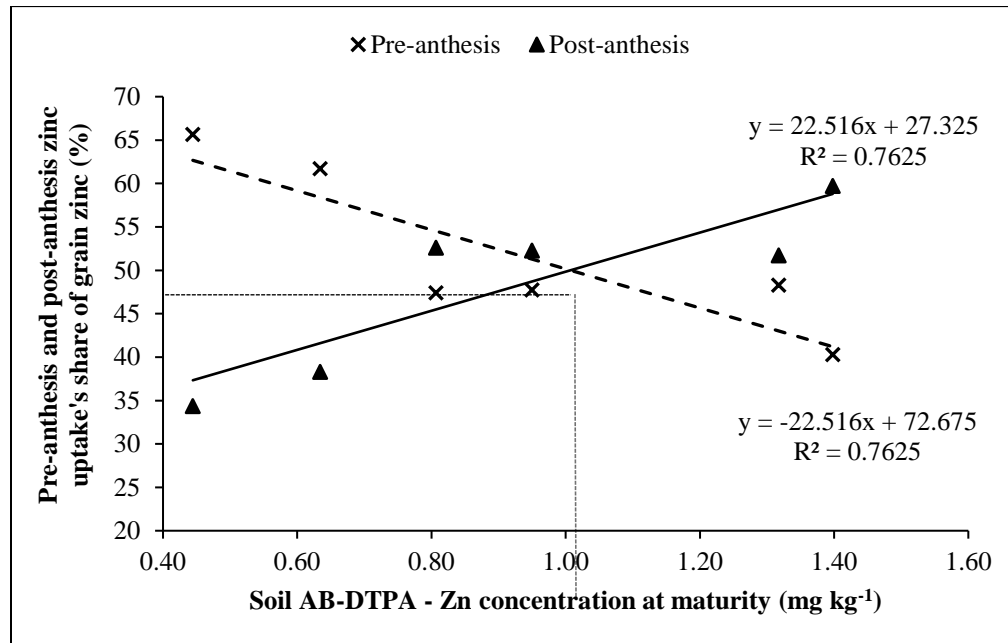


Figure 1. Relationship between soil AB-DTPA-Zn concentration at maturity and the proportion of rice grain Zn derived from pre-anthesis and post-anthesis uptake (%). The dotted vertical line represents the soil AB-DTPA-Zn concentration where Zn remobilization and Zn uptake contribute equally to grain Zn content.

DISCUSSION

The present field study examined the effects of soil zinc fertilization on Zn uptake at pre- and post-anthesis stages, and remobilization by the lowland rice. The rice genotype under investigation exhibited marked increase in most of the studied parameters when exposed to increasing Zn levels. This responsiveness indicates that the experimental soil was low to medium in available zinc. Soils having $< 0.5 \text{ ppm}$ of DTPA-extractable zinc are generally regarded as potentially deficient in zinc and may benefit from the application of zinc fertilizers (Chatterjee et al., 2018).

In our field experiment, rice yield and yield related characteristics (except tiller count per plant and panicle length) were increased significantly with utilization of Zn, which were in line with previous studies (Tharakan and Gite, 2018; Verma et al., 2022). Zn application causes a considerable increase in panicle length because Zn is necessary for meristematic cell development and division (Aslam et al., 2020). The increased panicle length and 1000-grain weight may be explained by zinc's role in critical metabolic processes such as ribosome activity, glucose metabolism, and chlorophyll production (Zulfiqar et al., 2021). Maximum panicle length, number of grains per panicle, and grain production were recorded by Khan et al. (2012) when Zn was applied at a rate of 9 kg ha^{-1} . Gomez-Coronado et al. (2016) observed a rise in the quantity of kernels in each panicle and 1000-grain weight, which they attributed to zinc's role in grain partitioning. Our investigation found that raising the Zn levels in the soil boosted the height of the rice plants, and Kadam et al. (2018) observed comparable results.

It has been demonstrated that adding zinc to the soil greatly increases biomass in terms of yields from shoots, grains, and straw (Table 2). Zinc's function in activating different enzymes, which starts early germination with a consistent crop stand and increases paddy production, may be the cause of this (Farooq et al., 2018). Additionally, zinc supplementation improves pollination and pollen tube growth, increases the number of kernels per panicle, and ultimately increases grain yield (Shariatipour et al., 2020).

Better zinc absorption in plants was made possible by the elevated zinc levels in the soil solution. According to Islam et al. (2021), the application of Zn fertilizers resulted in higher crop productivity and Zn concentration of different rice varieties. Higher Zn accumulation and improved mobilization of plant Zn reserves toward the grain were observed by Hussain et al. (2016), leading to the maximum Zn uptake in grain with greater Zn fertilization level. Zn addition to rice

crops by Zn fertilizers also increased the Zn content of the grains, according to reports from Rengel (2015). In the current study, zinc treatments enhanced Zn absorption in rice and enhanced grain quality by providing enough zinc in Zn deficient soil. Zn fertilizer applications, both soil and foliar, boost rice grain yield and Zn content; the benefits of application vary depending on native soil Zn availability, nitrogen fertilizer rate, and Zn fertilizer application technique (Guo et al., 2016). In the current study, the elevated Zn accumulation by rice straw can be linked to the inherently high Zn content present within the straw itself. Research has shown that a significant proportion of the total Zn accumulated by rice plants is concentrated in the straw. Remarkably, this proportion can constitute more than 60% of the total Zinc content in the entire rice plant (Yin et al., 2016; Verma et al., 2022).

In the current study, share of grain Zn provided by remobilization declined while that of post-anthesis uptake increased upon increasing Zn fertilization rate (Table 4), aligning with findings of Xu et al. (2021). Both newly absorbed zinc that is transported straight to the kernels during the grain-filling stage, avoiding intermediate storage in the shoot, and zinc that was previously absorbed, stored in the shoot, and then remobilized to the grain are the sources of the zinc concentration in the grain. The first source exhibits post-anthesis zinc uptake, whereas the second source exhibits pre-anthesis remobilization (Liu et al., 2022). After anthesis, plants have a harder time absorbing zinc when the soil or environmental circumstances limit their supply, which results in a lower amount of zinc being absorbed by the shoot. The remobilization of zinc from the vegetative components is therefore the main source of zinc in the grain. According to Yin et al. (2016), the main source of zinc in grain under Zn-sufficient conditions is zinc uptake by the shoot during grain filling. Persistent root absorption was the primary source of grain loading in nearly every genotype under Zn-sufficient conditions, as observed by Impa et al. (2013a). However, genotypes differed significantly in the main sources of grain Zn loading in Zn-deficient environments, indicating a higher level of genotypic variability for this characteristic. According to Stomph et al. (2014), the allocation of zinc obtained before and after flowering contributed roughly similar amounts to grain zinc for the rice accession under examination. Wu et al. (2010), on the other hand, found that a significant portion of the zinc deposited in the grains at maturity had been retranslocated from other plant parts rather than being transferred straight to the grains following uptake during the grain-filling stage. The different findings of these studies can be explained in term of genotypic differences. Certain Zn-efficient rice genotypes may be better able to transfer zinc from older to actively growing tissues than genotypes that are sensitive to zinc deficiency, according to Impa et al. (2013b).

The availability of soil zinc determines how much of the zinc accumulated in grains is attributable to pre-anthesis remobilization as opposed to post-anthesis shoot uptake, as mentioned by Liu et al. (2019) and corroborated by the results of our investigation (Table 4, Figure 1). The available soil zinc (AB-DTPA-Zn) concentration was identified as the primary source of zinc in the grain in this investigation; the essential threshold for the soil was 1.0 mg kg⁻¹ of AB-DTPA-Zn. Post-anthesis shoot uptake is imperative than remobilization when this value is surpassed; below this threshold, the opposite is true. It will be easier to direct zinc management techniques in rice production if this value in various soils is recognized. Johnson-Beebout et al. (2016), however, emphasized that critical Zn level for soil can be modified by the uptake behavior of rice genotypes. We were unable to assess the role of root uptake in the distribution of zinc among grains due to the lack of root data. Numerous physiological processes, including as root uptake, root to shoot transfer, internal retranslocation, and loading to grain, are responsible for the zinc content of crop grains. To precisely assess each physiological process's contribution to grain zinc loading, more research is needed.

CONCLUSION

Zinc fertilization had a notable influence on rice yield, Zn concentration and accumulation at both anthesis and maturity stages. More than 85% of the total zinc (grain + straw) accumulated at maturity originated from pre-anthesis uptake. Additionally, Zn remobilization efficacy and the grain share Zn derived from remobilization significantly dropped as zinc levels rose from 0 to 15 kg Zn ha⁻¹. Moreover, it was evident that post-anthesis uptake was the predominant source of grain Zn when AB-DTPA extractable zinc concentrations exceeded 1.0 mg kg⁻¹, while pre-anthesis remobilization prevailed at lower soil zinc concentrations. These findings will enhance our understanding of zinc uptake and remobilization in rice crops, aiding in the development of zinc management strategies to achieve higher yields and increased grain zinc content.

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AUTHOR CONTRIBUTIONS

All authors contributed equally to this research.

COMPETING OF INTEREST

The authors declare that the research was carried without any commercial or financial relationships that could be construed as a potential conflict of interest.

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